

# Long-term iceshelf-covered meiobenthic communities of the Antarctic continental shelf resemble those of the deep sea

Armin Rose · Jeroen Ingels · Maarten Raes ·  
Ann Vanreusel · Pedro Martínez Arbizu

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**Abstract** Since strong regional warming has led to the disintegration of huge parts of the Larsen A and B ice shelves east of the Antarctic Peninsula in 1995 and 2002, meiofaunal communities covered by ice shelves for thousands of years could be investigated for the first time. Based on a dataset of more than 230,000 individuals, meiobenthic higher taxa diversity and composition of Larsen continental shelf stations were compared to those of deep-sea stations in the Western Weddell Sea to see whether the food-limiting conditions in the deep sea and the food-poor shelf regime at times of iceshelf coverage has resulted in similar meiobenthic communities, on the premises that food availability is the main driver of meiobenthic assemblages. We show here that this is indeed the case; in terms of meiobenthic communities, there is greater similarity between the deep sea and the inner Larsen embayments than there is similarity between the deep sea and the former Larsen B iceshelf edge and the open continental shelf. We also show that resemblance to Antarctic deep-sea meiofaunal communities was indeed significantly higher for

communities of the innermost Larsen B area than for those from intermediate parts of Larsen A and B. Similarity between communities from intermediate parts and the deep sea was again higher than between those of the ice-edge and the open shelf. Meiofaunal densities were low at the inner parts of Larsen A and B, and comparable to deep-sea densities, again likely owing to the low food supply at both habitats. We suggest that meiobenthic communities have not yet recovered from the food-limiting conditions present at the time of iceshelf coverage. Meiofaunal diversity on the other hand seemed driven by sediment structure, being higher in coarser sediments.

**Keywords** Climate change · Iceshelf break-up · Metazoan meiofauna · Antarctic Peninsula · Larsen A · Larsen B · ANDEEP 2 · Deep sea

## Introduction

The opening of large ice shelves in the Larsen region east of the Antarctic Peninsula has enabled scientists to study what was hidden under the ice for centuries or even millennia. The Larsen B area was permanently ice-covered during the Holocene until recently (i.e. for more than 11,000 years; Domack et al. 2005a, 2007; doubted by Pudsey et al. 2006), whereas the Larsen A iceshelf probably disintegrated up to three times during this geological era (Domack et al. 2005a). Atmospheric warming in the region of the Antarctic Peninsula (Chapman and Walsh 2007; Solomon et al. 2007; Smale and Barnes 2008; Clarke et al. 2007) has been postulated to be the main cause of the collapse of these ice shelves in 1995 and 2002 (Vaughan and Doake 1996; Scambos et al. 2003). Still more than 30 % of the Antarctic continental shelf lies beneath ice (Barnes and Peck 2008), but ice shelves have been retreating continuously during the last decades owing to

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A. Rose  
BioConsult SH GmbH & Co KG, Schobüller Str. 36,  
D-25813 Husum, Germany

J. Ingels (✉)  
Plymouth Marine Laboratory, Prospect Place, The Hoe, PL1 3DH,  
Plymouth, UK  
e-mail: jein@pml.ac.uk

M. Raes · A. Vanreusel  
Marine Biology Section, Biology Department, Ghent University,  
B-9000 Ghent, Belgium

P. M. Arbizu  
Senckenberg am Meer Wilhelmshaven, Dept DZMB,  
D-26382 Wilhelmshaven, Germany

climate change (Cook et al. 2005; Braun et al. 2009). Significantly rising summer ocean temperatures near the Western Antarctic Peninsula (Meredith and King 2005; Rignot et al. 2014) may have caused the break-up of the Wilkins Ice Shelf (Braun et al. 2009), and latest reports show that the Thwaites Glacier on the West Antarctic Peninsula is on the brink of collapse for the same reason (Joughin et al. 2014).

Benthic communities of Antarctic shelf areas that have been covered by ice shelves for thousands of years are most likely impoverished compared to open-shelf communities before iceshelf formation, or compared to the often rich open-shelf communities found today (Gutt et al. 2011). The long period of food and light limitations, which resemble conditions in deep-sea environments (e.g., Thistle 2003; Giere 2009), may have caused partial loss of the open-shelf fauna, while at the same time invading deep-sea species that were better adapted may have outcompeted local fauna over a period of thousands of years (Thatje et al. 2005; Post et al. 2011). These exchange processes on community level might be partly reversible after iceshelf break-ups, but a faunal resemblance with the deep sea is assumed to persist many years after iceshelf disintegration owing to the slow colonization rates of some taxa (Raes et al. 2010). These processes are ongoing, and the Antarctic shelf benthos is considered as still being recolonized following the last glaciations (Gutt 2006).

The limited data on life under ice shelves suggest the presence of a gradient from rich communities on the open shelf (e.g., Gutt and Starman 1998: megabenthos in the Weddell and Lazarev Seas) to impoverished ones under permanent ice cover (e.g., Azam et al. 1979: bacteria, microplankters and zooplankters under the Ross Ice Shelf). Recent community studies for the Larsen A and B areas confirm this hypothesis (Raes et al. 2010; Hauquier et al. 2011: nematodes and other benthic organisms; Gutt et al. 2011: meio-, macro-, and megafauna; Gutt et al. 2013: megabenthos), and earlier studies on the life under the Ross Ice Shelf also suggest the presence of such a gradient (Bruchhausen et al. 1979; Lipps et al. 1979: fish and invertebrates of the sub-shelf benthos). Furthermore, Holm-Hansen et al. (1979) showed that, in the Ross Ice Shelf area, organic matter of phytodetrital origin was nearly absent from the sediments, whilst under the Amery Ice Shelf, 100 km away from open water, a diverse benthic assemblage was found being supported by food particles transported by strong advective currents (Post et al. 2007; Riddle et al. 2007).

Probably the richest elements of Southern Ocean biodiversity, meiofauna and microbes, are the least well known (Kaiser et al. 2013). A seafloor area smaller than a beer coaster may contain more than 60 different, mostly unknown, species of meiobenthic copepods or nematodes (e.g., Rose et al. 2005; De Mesel et al. 2006; Ingels et al. 2006; Brandt et al. 2007). Generally, nematodes dominate Antarctic shelf and deep-sea

meiobenthic communities numerically, followed by copepods (e.g., Herman and Dahms 1992; Vanhove et al. 1995; Fabiano and Danovaro 1999), although protozoan foraminiferans can also dominate communities (Cornelius and Gooday 2004). Despite the recent increase in scientific reports, our understanding of meiofauna communities in Antarctica remains limited, owing to sparse sampling effort and the taxonomical expertise required (Ingels et al. 2014a; exceptions: e.g., Gutzmann et al. 2004; De Mesel et al. 2006; Brandt et al. 2007; Gheerardyn and Veit-Köhler 2009; Ingels et al. 2010; Hauquier et al. 2011).

For the deep sea, the meiobenthos is ecologically and biologically distinct from other size fractions (Thistle 2003), owing to evolutionary mechanisms that determine the size structure of species pools with implications for dispersal, development, and generation time, as well as resource partitioning and feeding. By their size, meiobenthic organisms are inherently adapted to passive feeding of small deposit particles, which is energetically favorable in the deep sea and allows a high degree of trophic partitioning and diversification for small organisms (Giere 2009). Food resources (productivity regimes) are an important driver of meiobenthic communities with lower food availability reflected in lower meiofaunal standing stocks for different Antarctic continental shelf environments (Herman and Dahms 1992; Vanhove et al. 1995; Fabiano and Danovaro 1999), as well as bathyal and hadal locations (e.g., Thistle 2003; Brandt et al. 2007). Also, within single deep-sea basins, meiobenthic community composition and density might differ significantly when productivity differs on different spatial scales (Rose et al. 2005; Sebastian et al. 2007). These examples of resource dependence across different depth ranges suggest that food conditions override depth patterns (and correlated depth-dependent environmental gradients) in structuring Antarctic meiobenthic communities. Consequently, iceshelf-covered shelf sediments with similar food paucity as observed in the deep sea may harbour meiobenthic communities resembling those found in deep-sea environments (except for chemosynthetically driven ecosystems which are energetically not dependent on phytodetrital input). With this in mind, the recently opened Antarctic Larsen Ice Shelf region offered the chance to study benthos that has been experiencing low-productivity conditions for thousands of years until the recent iceshelf collapse, and allowed comparing faunal assemblages from the Larsen area with those of the nearby food-poor deep sea.

In this study, we tested whether meiobenthic sub-iceshelf continental shelf communities are more similar to deep-sea communities than they are to continental shelf communities at the ice edge and in open waters, under the premises that ice-covered and deep-sea environments both experience low food input from the upper water column. We compared seven continental shelf stations from the Larsen A and B areas and Elephant Island to four stations from a nearby deep-sea

transect in the Western Weddell Sea. Continental shelf and deep-sea stations were sampled in different years, but we did not consider this a major problem due to the general stability of deep-sea environments.

The diversity and role of environmental factors in structuring meiobenthic distribution patterns at each of the investigated stations were also analyzed, in order to account for the complexity of benthic communities which should not be obscured by a simplification inherent to all tests on significant differences. The results of this study contribute considerably to our understanding of biodiversity and functioning of the benthic ecosystem in one of the most remote places on earth.

## Materials and methods

### Faunal compartment

We focused on metazoan meiobenthos (all sediment organisms that pass through a 1000- $\mu\text{m}$  sieve and are retained on a 40- $\mu\text{m}$  sieve). This size definition meant that we extracted permanent (whole life cycle within the 40–1000  $\mu\text{m}$  size range), as well as temporary members (part of life cycle within 40–1000  $\mu\text{m}$  only) of the meiofauna, an approach applied in most Antarctic meiofaunal studies (e.g., Herman and Dahms 1992; Fabiano and Danovaro 1999; Lee et al. 2001a, b; Vanhove et al. 1995, 2004). Applying a size-based approach (rather than ‘taxonomical membership’) is ecologically sound, because (1) the meiofaunal compartment is known to be clearly distinct from other size-based compartments of marine communities (Thistle 2003), (2) size restrictions of meiofaunal organisms pose limitations on the range of suitable food particles and sediment grain size, bringing ecological relevance in terms of feeding ecology and colonization processes (Giere 2009), and (3) the strict size definition of meiofauna is less prone to inconsistencies than other approaches and increases comparability between studies, habitats and ecosystems. On the other hand, the size definition may lead to problems of comparability between studies, habitats and ecosystems, if organisms grow larger with an increased availability of food. Furthermore, protozoan meiofauna had to be excluded here because of special methodological requirements to study these organisms (e.g., Cornelius and Gooday 2004).

### Sampling design

Repeated multicorer (MUC) deployments were conducted at six continental shelf stations in the Larsen A and B region east of the Antarctic Peninsula (‘B West’, ‘B South’, ‘B North’, ‘B East’, ‘A South’: all at 242–427 m depth); ‘B Seep’: a cold-seep station at 820 m depth situated in a trough (Niemann et al. 2009; Hauquier et al. 2011); (Fig. 1; Table 1); and at one open continental shelf reference station near Elephant Island

(‘Elph’: 410 m depth) during cruise ANT-XXIII/8 (RV *Polarstern* PS69, November 2006–January 2007; Gutt 2008). Four Western Weddell Sea deep-sea stations (‘A1000’, ‘A2000’, ‘A3000’, ‘A4000’: depth-transect from 1080 m to 4070 m; Fig. 1; Table 1) were sampled during the ANDEEP-2 campaign (Antarctic benthic DEEP-sea biodiversity; RV *Polarstern* PS61 ANT-XIX/4, March 2002). None of the data used here have so far been published. An overview of sampling stations is given in Table 1.

## Hypotheses

Regarding our sampled stations, the following general hypotheses were proposed:

Owing to the longer-term effects of low productivity and food supply, the meiobenthic community of a formerly iceshelf-covered and sheltered innermost Larsen B shelf station (‘B West’) shows higher affinity to communities at four deep-sea stations of different depth ( $A_{a-d}$ : ‘A1000’, ‘A2000’, ‘A3000’, ‘A4000’) than is the case for three Larsen A and B stations at intermediate distances to the former ice edge (‘A South’, ‘B North’, ‘B East’), and for an inner and deeper but more productive Larsen B cold seep station (‘B Seep’). Meiobenthic communities from the latter four stations show a higher affinity to deep-sea communities than do those from a station near the former Larsen B ice edge (‘B South’) and from a continental shelf reference station near Elephant Island (‘Elph’).

In detail, pairs of null and alternative hypotheses,  $I-XIV_{a-d}$  ( $H_0$  only shown for first hypothesis), were specified according to these assumptions. Hypotheses were based on pairwise comparisons between core-scale similarities of meiobenthic higher taxa community composition from the supposedly low-productive continental shelf station ‘B West’, the higher-productive shelf stations ‘B South’ and ‘Elph’, or one of the four intermediate shelf stations,  $Int$  (‘A South’, ‘B North’, ‘B East’, ‘B Seep’), and community composition at one of four deep-sea stations,  $A_{a-d}$  ( $Sim_{Y;Aa-d}$ ):

Assumed low versus high food supply:

$$\begin{aligned} I_{a-d} \quad H_A : Sim_{BWest;Aa-d} &> Sim_{BSouth;Aa-d} \\ (H_0 : \quad \quad \quad Sim_{BWest;Aa-d} &\leq Sim_{BSouth;Aa-d}) \\ II_{a-d} \quad H_A \quad Sim_{BWest;Aa-d} &> Sim_{Elph;Aa-d} \end{aligned}$$

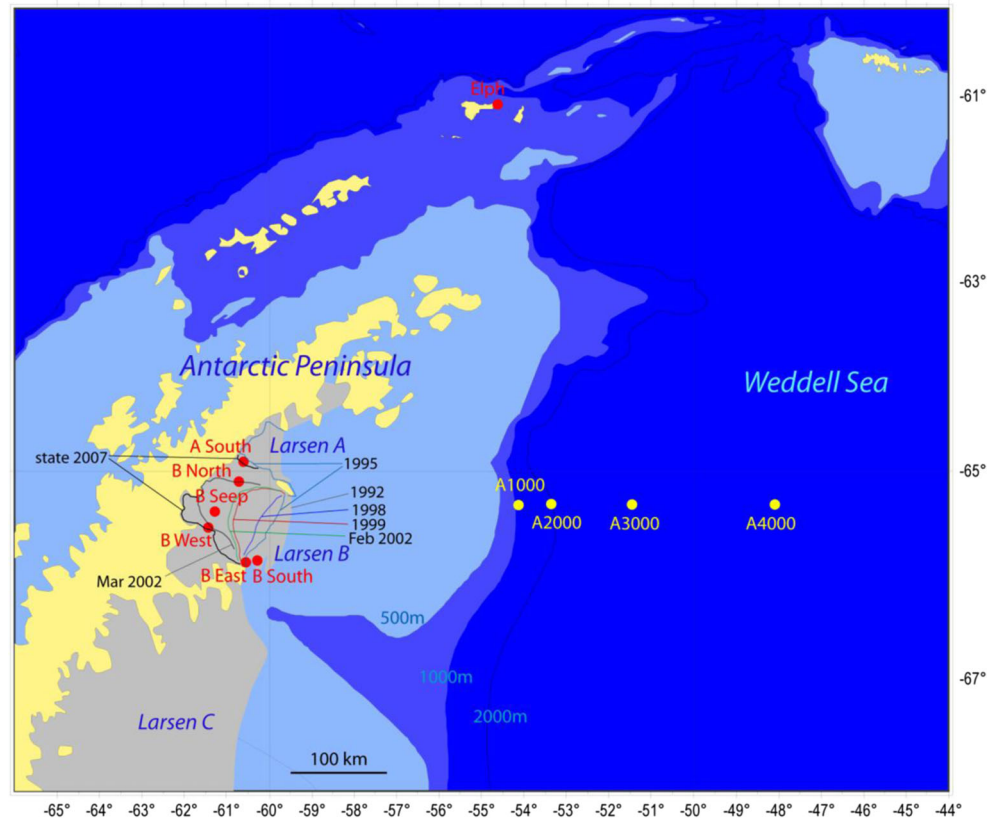
Assumed low versus intermediate food supply:

$$III-VI_{a-d} \quad H_A : \quad Sim_{BWest;Aa-d} > Sim_{Int;Aa-d}$$

Assumed intermediate versus high food supply:

$$\begin{aligned} VII-X_{a-d} \quad H_A : \quad Sim_{Int;Aa-d} &> Sim_{BSouth;Aa-d} \\ XI-XIV_{a-d} \quad H_A : \quad Sim_{Int;Aa-d} &> Sim_{Elph;Aa-d} \end{aligned}$$

**Fig. 1** Sampling sites in the Larsen A and B region (Jan 2007; red dots), near Elephant Island (Dec 2006; red dot), and in the Western Weddell Sea (ANDEEP 2, Mar 2002; yellow dots); also shown is the episodic iceshelf retreat in the Larsen A and B region since 1992



### Processing of sediment samples

Sediment samples (25.52 cm<sup>2</sup> surface, 127.6 cm<sup>3</sup> volume) with intact sediment-water interface were collected with a MUC (12 cores; Barnett et al. 1984). Several MUC deployments were conducted at each station, with one to three cores taken from each deployment (Table 1). In total, 59 cores from Larsen A and B, three cores from Elephant Island, and 24 deep-sea cores from the Western Weddell Sea were analyzed (in total 86 cores; Table 1). The sediment fraction and supernatant water was preserved in 4–7 % buffered formaldehyde. The samples were subsequently washed through a 1-mm sieve with tap water and retained on a 40- $\mu$ m sieve. Centrifugation with a colloidal silica polymer (Levasil<sup>®</sup>) as flotation medium and kaolin to cover the heavier particles (McIntyre and Warwick 1984) was repeated three times at 4000 rpm for 6 min. After each centrifugation, the floating matter was decanted and rinsed with tap water. Metazoan meiofauna organisms were sorted under a stereomicroscope ( $\times 50$  magnification) and identified to higher taxon level following Higgins and Thiel (1988), whereby copepod adults and nauplius larvae were separated because of their ecological distinctness according to size and food (e.g., Decho and Fleeger 1988).

Grain size analysis of extra cores from each MUC haul was carried out after disaggregation using laser diffraction (Malvern Mastersizer 2000; Malvern Instruments,

Worcestershire, UK). The sediment depth at which a color change concomitant with sulphidic smell occurred was measured. This was used as a rough estimate for beginning anoxia, and the proportion of such sediment in the upper 30 cm was taken as an environmental variable ('anox\_cm\_in\_up30cm').

Phytopigment concentrations were obtained in different ways. To estimate the amount of primary organic matter reaching the deep-sea floor, the sum of the chlorophyll a and phaeopigment concentration ( $\mu$ g/g CPE) of the deep-sea samples was measured for the first cm of sediment with a fluorometer following Shuman and Lorenzen (1975). For the Elephant Island and Larsen samples, phytopigment concentrations ( $\mu$ g/g CPE in the upper 5 cm of sediment) were obtained by HPLC analysis (supernatant extracted from the lyophilized sediment by adding 10 ml of 90 % acetone). Chlorophyll a and c, as well as phaeophytin a and c inventories of the upper 11 cm of sediment, were provided by a study of Sañe Schepisi et al. (2011).

### Statistical analyses

Similarity analyses were performed according to meiobenthic higher taxa composition, using the Bray–Curtis similarity coefficient (BC; Bray and Curtis 1957, sensu Somerfield 2008). Computations and nMDS (non-metric multidimensional scaling) plots were performed by free statistical software R v.3.0.0 (R Core Team 2013) and package

**Table 1** Geographical coordinates (WGS84), sampling date, and depth of the studied Larsen A and B, Elephant Island, and ANDEEP-2 stations (1–5 deployments per station, 1–3 cores per deployment; a multicorer (Barnett et al. 1984) with 57-mm inner diameter of tubes was used)

Station	Deploym.	Cores	Date	Latitude	Longitude	Depth (m)
Larsen: 'B South'	PS69/700-8	3	12.01.07	65°54.98' S	60°20.54' W	422
	PS69/700-9	3	12.01.07	65°54.95' S	60°20.88' W	417
	PS69/702-4	2	12.01.07	65°55.12' S	60°19.96' W	427
	PS69/702-7	3	12.01.07	65°54.49' S	60°21.37' W	405
	PS69/702-8	3	12.01.07	65°54.95' S	60°20.95' W	410
Larsen: 'B West'	PS69/710-2	2	16.01.07	65°33.03' S	61°36.98' W	277
	PS69/710-3	3	16.01.07	65°33.04' S	61°37.18' W	281
	PS69/710-7	3	16.01.07	65°33.03' S	61°37.01' W	275
	PS69/710-8	2	16.01.07	65°33.03' S	61°37.00' W	283
	PS69/710-9	3	16.01.07	65°33.07' S	61°37.06' W	288
Larsen 'B Seep'	PS69/706-5	2	15.01.07	65°26.09' S	61°26.48' W	819
	PS69/706-6	2	15.01.07	65°26.10' S	61°26.53' W	820
	PS69/709-5	3	15.01.07	65°26.09' S	61°26.51' W	819
	PS69/709-7	3	15.01.07	65°26.07' S	61°26.48' W	818
	PS69/709-8	3	15.01.07	65°26.07' S	61°26.49' W	818
Larsen: 'B North'	PS69/715-2	3	18.01.07	65°06.39' S	60°45.04' W	308
	PS69/715-4	3	18.01.07	65°06.44' S	60°45.07' W	307
	PS69/718-1	3	19.01.07	65°06.33' S	60°45.17' W	306
	PS69/718-3	1	19.01.07	65°06.43' S	60°44.93' W	303
	PS69/718-5	3	19.01.07	65°06.40' S	60°45.60' W	304
Larsen: 'B East'	PS69/721-4	1	20.01.07	65°55.55' S	60°37.77' W	370
Larsen: 'A South'	PS69/723-1	2	22.01.07	64°56.07' S	60°38.57' W	242
	PS69/723-2	3	22.01.07	64°56.06' S	60°38.58' W	242
Elephant Isl.: 'Elph'	PS69/609-5	1	20.12.06	61°09.03' S	54°32.28' W	410
	PS69/609-7	1	21.12.06	61°07.99' S	54°31.15' W	412
	PS69/609-8	1	21.12.06	61°08.04' S	54°31.36' W	400
ANDEEP 2: 'A1000'	PS61/133-6	1	07.03.02	65°20.20' S	54°14.30' W	1085
	PS61/133-8	3	07.03.02	65°20.20' S	54°14.30' W	1107
	PS61/133-10	2	07.03.02	65°20.20' S	54°14.30' W	1109
ANDEEP 2: 'A2000'	PS61/132-5	3	06.03.02	65°17.70' S	53°22.80' W	1978
	PS61/132-7	3	06.03.02	65°17.70' S	53°22.80' W	2076
	PS61/132-8	1	06.03.02	65°17.70' S	53°22.80' W	2074
ANDEEP 2: 'A3000'	PS61/131-7	3	06.03.02	65°19.50' S	51°31.00' W	3057
	PS61/131-9	1	06.03.02	65°18.50' S	51°31.90' W	3064
	PS61/131-11	1	06.03.02	65°18.70' S	51°30.90' W	3068
ANDEEP 2: 'A4000'	PS61/134-6	3	09.03.02	65°19.90' S	48°05.60' W	4068
	PS61/134-8	3	09.03.02	65°19.90' S	48°05.60' W	4063

'vegan' v.2.0–7 (Oksanen et al. 2013). The BC with its emphasis on abundance values (Pfeifer et al. 1998) was preferred because abundance differences were considered as being most important in the context of productivity levels and food conditions which lead to quantitative rather than qualitative community differences (Pfannkuche 1985). Abundances were square-root transformed in order to reduce a dominance effect of nematodes. Non-parametric Wilcoxon Mann–Whitney *U* tests (Mann and Whitney 1947) were performed for hypothesis testing by comparing two groups of similarity values ( $\alpha = 5\%$ ), using free statistical software R

v.3.0.0. Tests were performed on BC similarities of all pairwise combinations of cores from the continental shelf stations, with the cores from each of the four deep-sea stations, resulting in 56 tests. Results were corrected for multiple testing by usage of the FDR (False Discovery Rate) after Benjamini and Hochberg (1995).

Prior to hypothesis testing, we investigated whether within-deployment (pseudoreplicates) core similarities differed significantly from between-deployment (true replicates) core similarities, in order to evaluate if all cores available for a station could be pooled for our analyses. A two-way nested

ANOSIM (Clarke and Green 1988), conducted with software PRIMER v.6.1.6 (Clarke and Warwick 2001), indicated that the variance among cores from single deployments was not significantly different from the variance among cores from different deployments at the same station ( $R=-0.058$ ,  $p=0.789$ ). In addition, a Wilcoxon Mann–Whitney  $U$  test showed no significant differences between BC similarities obtained from pairs of cores within single MUCs and pairs of cores from different MUC deployments within a station. An  $F$  test on variances between these two groups again showed no significant difference. Finally, a Mantel correlogram (not shown), comparing the community dissimilarity matrix to a geographical distance matrix on core level, gave evidence that spatial dependence of meiofauna composition remained very similar from within-MUC scale (1 m) to a scale of several km distance between cores. All these results indicated that pooling of cores collected at a certain station did not pose spatial autocorrelation and hence pseudoreplication issues. This allowed a grouping of cores from different deployments within a certain station, which greatly enhanced the power of subsequent tests (Clarke and Warwick 2001).

Diversity was analyzed by a richness index (Shannon's  $H'$ ; Shannon and Weaver 1949), a dominance-driven evenness index (Simpson's Evenness  $1-\lambda$ ; Simpson 1949), and the rarefaction method (modified rarefaction model after Hurlbert 1971), using software PRIMER v.6.1.6 (Clarke and Warwick 2001). In order to uncover what might have caused the obtained values of diversity and of other measures of community structure (number of meiofaunal higher taxa,  $T$ , and individuals per core,  $N$ ), linear regressions of these community parameters on environmental factors of interest available for all stations (depth, sediment structure) were performed and tested for significance ( $\alpha = 5\%$ ) with software KYPLOT v.2.0 beta 15 (free software, © 1997–2001; Koichi Yoshioka, Japan).

Canonical correspondence analyses (CCA) were performed for assessment of correlations between assemblage structures, stations, and environmental factors (Ter Braak 1986; Jongman et al. 1995; discussed by Legendre and Gallagher 2001), with software MVSP 3.13b (Kovach Computing Services, 2002). The CCA ordination technique performs multiple regressions of dependent variables (taxa scores, site scores) on independent variables (environmental factors) by reciprocal averaging (Ter Braak 1986), whilst assuming a unimodal abundance distribution along environmental gradients. Data were square-root transformed and rare taxa were down-weighted. Results were visualized by triplots which combined taxa scores, site scores and environmental vectors (e.g., Legendre and Gallagher 2001). Major questions to be answered with the CCA analyses were, (1) what proportion of variation within the meiofauna dataset was explainable by the measured environmental factors, (2) which factors showed highest correlations to certain canonical axes and to

site scores constrained by meiobenthic higher taxa composition, and (3) are there certain higher taxa that favor certain conditions. Answering these specific questions facilitated the interpretation of the meiofaunal community patterns observed at our stations.

A total of 14 environmental factors were considered for CCA: seven grain size variables of the upper cm of sediment (clay %, silt %, very fine sand %, fine sand %, medium sand %, coarse sand %, and very coarse sand %), depth of sediment color change (concomitant with sulphidic smell in the upper 30 cm of sediment), station water depth, and five phytopigment variables ( $\mu\text{g/g}$  CPE in the upper five cm of sediment by HPLC; chlorophyll a and c and phaeophytin a and c in the upper 11 cm of sediment; after Sañe Schepisi et al. 2011). Regarding productivity measures, CPE concentrations of sediment samples from the ANDEEP-2 stations were obtained by a method different from that used for the Elephant Island and Larsen samples. Therefore, CPE concentrations of the former samples were not considered as environmental variables for canonical correspondence analyses (CCA). Due to this, a first CCA (A) was computed which included all environmental variables, but with the cost having to reduce the number of stations to avoid incomparable data. A second CCA (B) included all stations, but in this case the number of environmental variables had to be reduced.

## Results

### Community similarity analysis and tests of hypotheses

Regarding hypotheses *I* and *II*, Wilcoxon Mann–Whitney tests showed that core-wise Bray–Curtis similarity between meiofaunal communities from the sheltered innermost Larsen station ‘B West’ and the four deep-sea stations ‘A1000’ to ‘A4000’ was always significantly higher ( $p < 0.001$ ) than similarity between the deep-sea stations and the former Larsen ice-edge station ‘B South’ and the open shelf station near Elephant Island, ‘Elph’ (Table 2). This led to the rejection of  $H_0$ .

As to hypotheses *III–VI*, the results were a bit more ambiguous. BC similarity of the innermost station ‘B West’ to the four deep-sea stations was still always significantly higher ( $p < 0.05$ ) compared to similarity of the intermediate Larsen stations ‘B North’, ‘B Seep’, and ‘A South’ to the deep-sea stations, leading to the rejection of  $H_0$  for hypotheses *IV–VI* (Table 2). However, ‘B East’ was not significantly different from ‘B West’ in terms of their similarity to the deep-sea stations. Hence,  $H_0$  could not be rejected for hypothesis *III*.

Regarding hypotheses *VII–XIV*, the test outcome was again consistent. For 30 out of 32 tests, BC similarities between the intermediate Larsen stations ‘B North’, ‘B Seep’, ‘A South’ and

**Table 2** Tests of hypotheses I–XIV (see “Introduction”) regarding relative similarities of meiofaunal higher taxa composition of Antarctic shelf stations to each of four ANDEEP-2 deep-sea stations; a rejection of thenull hypothesis is marked by 1–3 asterisks ( $p$  values lower than 5 %, 1 %, or 0.1 %, respectively, after FDR correction for multiple testing)

Similarity innermost Larsen shelf – deep sea > Similarity ice edge and open shelf – deep sea			Similarity innermost Larsen shelf – deep sea > Similarity intermediate Larsen shelf – deep sea					
Hypoth.	I	II	Hypoth.	III	IV	V	VI	
$H_A$	B West > B South	B West > Elph	$H_A$	B West > B East	B West > B North	B West > A South	B West > B Seep	
A1000	0.000***	0.000***		0.828 ns	0.045*	0.005**	0.000***	
A2000	0.000***	0.000***		0.543 ns	0.001***	0.000***	0.000***	
A3000	0.000***	0.000***		0.229 ns	0.041*	0.018*	0.000***	
A4000	0.000***	0.000***		0.152 ns	0.005**	0.005**	0.000***	
Similarity intermediate Larsen shelf – deep sea > Similarity Larsen ice edge and open shelf – deep sea								
Hypoth.	VII	VIII	IX	X	XI	XII	XIII	XIV
$H_A$	B East > B South	B North > B South	A South > B South	B Seep > B South	B East > Elph	B North > Elph	A South > Elph	B Seep > Elph
A1000	0.000***	0.000***	0.000***	0.000***	0.005**	0.000***	0.009**	0.364 ns
A2000	0.001***	0.000***	0.026*	0.000***	0.007**	0.000***	0.525 ns	0.043*
A3000	0.007**	0.000***	0.000***	0.000***	0.016*	0.000***	0.000***	0.012*
A4000	0.001**	0.000***	0.000***	0.000***	0.015*	0.000***	0.000***	0.036*

A rejection of the null hypothesis is marked by \*, \*\*, or \*\*\* for  $p$  values lower than 5 %, 1 %, or 0.1 %, respectively, after FDR correction for multiple testing; ns not significant

the four deep-sea stations were significantly higher ( $p < 0.05$ ) than similarities between the former Larsen ice-edge station ‘B South’, the open shelf station ‘Elph’ and the deep-sea stations, leading to the rejection of  $H_0$  in these cases.

An nMDS plot of all investigated MUC cores (BC similarity of square-root transformed data) showed no strict separation of stations, although cores belonging to the same station were often aggregated (Fig. 2). The cores of ‘B West’ and the deepest shelf station ‘B Seep’ showed some overlap with the deep-sea stations, whereas the cores of ‘B South’ and ‘Elph’ did not overlap with the deep-sea stations at all, confirming the results of the Wilcoxon Mann–Whitney tests.

Furthermore, meiobenthic BC similarities of the four deep-sea stations to all continental shelf stations were evaluated by averaging resemblance values for all possible pairs of cores (Fig. 3). The sequence of resemblance of continental shelf to deep-sea stations was mostly consistent across the 1000–4000 m depth gradient (‘B West’ > ‘B East’ > ‘B North’ > ‘A South’ > ‘B Seep’ > ‘Elph’ > ‘B South’), indicating that the high resemblance of ‘B West’ and the low resemblance of ‘B South’ to the deep-sea stations were at either end of the resemblance spectrum between the continental shelf stations and the deep sea. Surprisingly, the deepest Larsen station ‘B Seep’ (800 m) showed only intermediate resemblance to the deep-sea stations.

#### Community composition

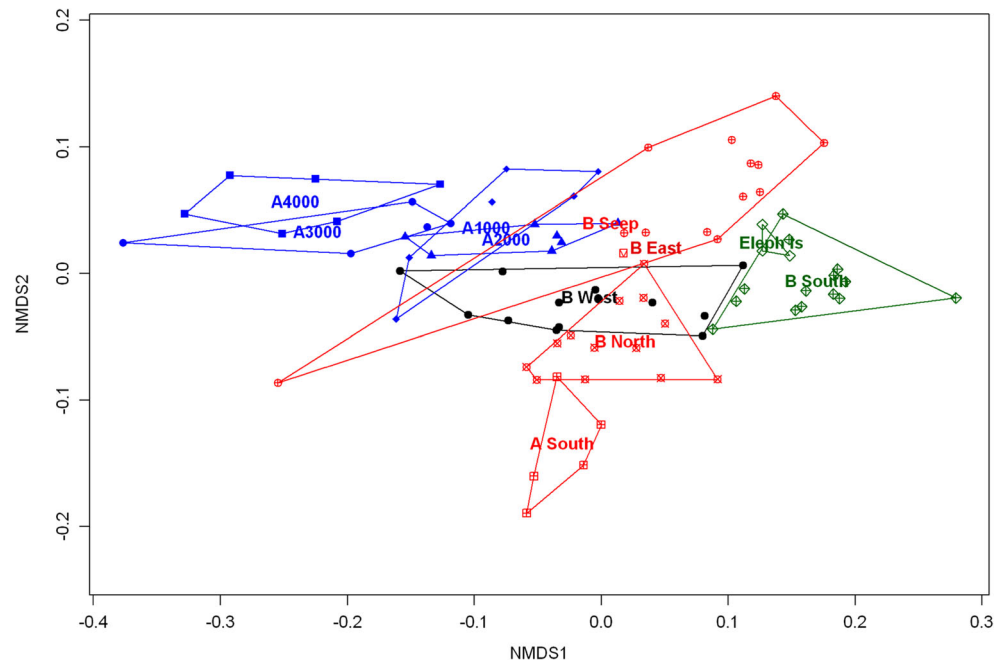
In total, 230,070 individuals belonging to 23 metazoan meiofaunal higher taxa were recorded (Table S1).

Communities were dominated by nematodes (202,119) and copepods (10,479 adults/copepodites; 13,088 nauplii). The remaining taxa comprised 4,384 individuals.

After logarithmic dominance classification following Engelmann (1978), nematodes were eudominant (>32 %) at all stations (see Table S1). Their dominance values at station level (pooled cores) ranged from 69.38 % at station ‘A South’ to 94.67 % at station ‘B Seep’, with the majority of values around 90 % (median: 89.17 %). Copepods (adults/copepodites) and nauplii followed, being dominant (>10 %) at ‘A South’ and subdominant (3.2–10 %) at most other stations (median for copepods: 4.62 %; for nauplii 4.42 %). At station ‘Elph’, however, copepods were less abundant (1.85 %) (i.e., recedent: 1.0–3.1 %). All other taxa were much less abundant or rare (i.e., subrecedent and sporadic: below 1 %) at all stations. Since dominance values are relative measures which depend on the abundances of other groups, a high proportion of rare taxa was partly attributable to high nematode abundances at most stations.

The degree of patchiness of higher taxa distributions among sites was estimated by the median-to-mean ratio (Table S1). A ratio lower than 1.0 indicated a left-skewed distribution and therefore a certain degree of patchiness at the station scale. Taking into account only taxa with >50 individuals, a low degree of patchiness (ratio between 0.9 and 1.0) was recorded for Copepoda (adults/copepodites as well as nauplii) and Annelida. Moderate patchiness (ratio between 0.5 and 0.9) was found for Nematoda, Loricifera, Ostracoda, and Acari. A high degree of patchiness (ratio between 0.5 and 0.3) was recorded for Bivalvia, Cnidaria,

**Fig. 2** NMDS plot of meiofaunal similarities (higher taxa composition, Bray–Curtis, square-root transformation) of 86 investigated multicorer cores from eleven stations (ANDEEP 2: blue; innermost Larsen B: black; intermediate Larsen B: red, Larsen B former ice edge and Elephant Island: green; stress = 0.1); hulls for better visualisation of stations



Kinorhyncha, and Rotifera. Finally, a very high patchiness (ratio below 0.3) was shown for Tanaidacea, Tantulocarida, Tardigrada, and Turbellaria.

#### Diversity analysis

In order to evaluate metazoan meiofauna diversity, the number of observed taxa ( $T$ ) and individuals ( $N$ ), Shannon's  $H'$  ( $\log e$ ) richness index, and Simpson's Evenness  $1-\lambda'$  were analyzed on core scale for all stations (Table S2). To reduce sample size bias (different number of cores per station), rarefaction analyses were also performed on station scale (pooled cores), which was not possible for the other indices.

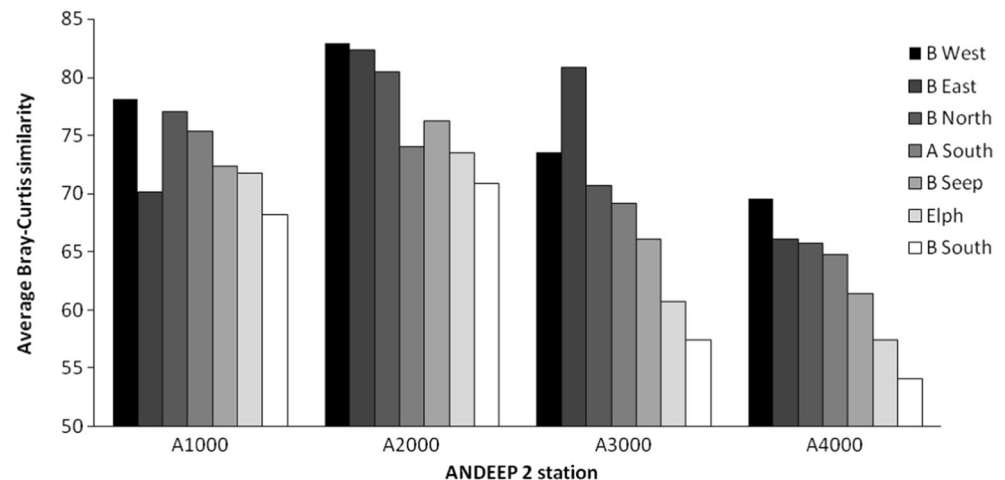
Highest taxon richness was observed at stations 'B South', 'Elph', 'A South', and 'A1000' (10 to 15 taxa per core). Taxa counts for the other stations were much lower (mostly <10,

down to 5 taxa per core; Fig. 4a). Only 13 higher taxa were found in 13 cores from the innermost Larsen B station 'B West', and 11 higher taxa in 13 cores from 'B Sep'. A higher richness was found at 'B South', 'A South', 'A 1000', and 'Elph', with 21 taxa (14 cores), 17 taxa (5 cores), 19 taxa (6 cores) and 18 taxa (3 cores), respectively.

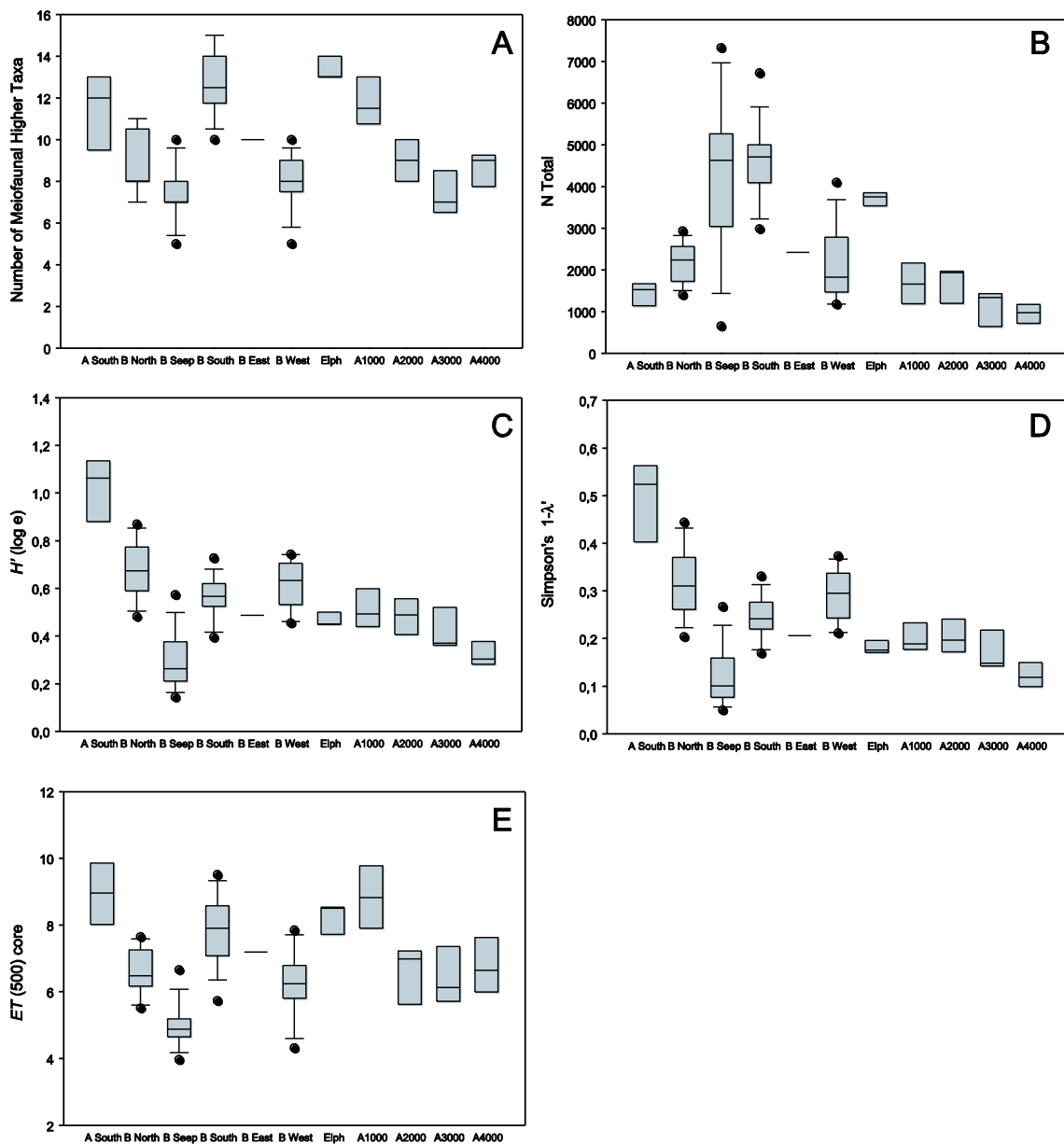
Meiofauna densities were highest at 'B South', 'B Sep', and 'Elph' (mostly between 3000 and 6000 individuals per core), whereas for the other stations 3000 individuals per core was rarely exceeded (Fig. 4b; see also densities per 10 cm<sup>2</sup> in Table S1, and median densities per core in Table S2).

Although emphasizing different aspects of diversity, Shannon's  $H'$  and Simpson's  $1-\lambda'$  yielded very similar results on core scale. Highest meiobenthic diversity was observed at 'A South', and lowest at 'B Sep' (Fig. 4c, d). The deep-sea stations showed decreasing diversity with increasing depth.

**Fig. 3** Core-scale resemblance of meiofaunal higher taxa composition of seven shelf stations from the Larsen region and Elephant Island to four deep-sea depth-transect stations from the Western Weddell Sea (ANDEEP 2: 'A1000' to 'A4000'); shelf stations are roughly ordered according to decreasing average Bray–Curtis similarities with deep-sea stations (mean of inter-station core-wise comparisons)







**Fig. 4** Box-Whisker plots showing medians (*line in the box*), 25th and 75th percentiles (*box*), 10th and 90th percentiles (*outer lines*), and counts outside the latter percentiles (*dots*); note that for seven stations not enough cores were available to calculate 10th and 90th percentiles (see Table S1); **a** number of meiofaunal higher taxa *T* per core for all stations; **b** number

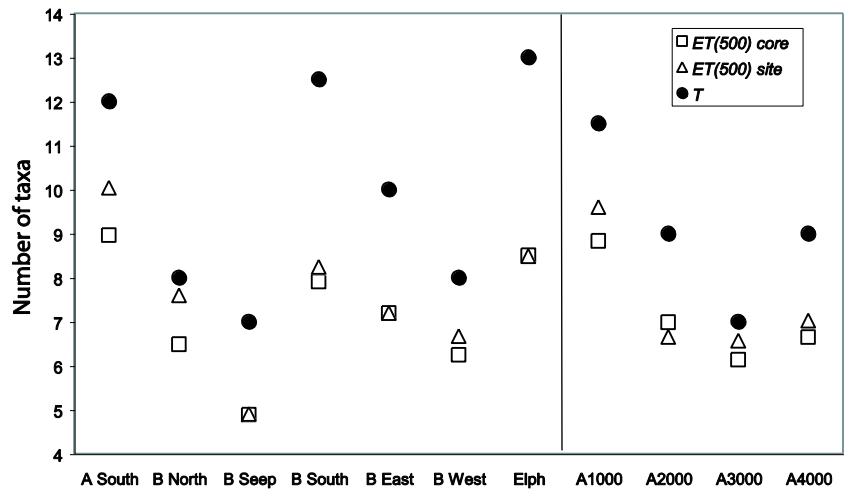
of meiofaunal individuals *N* per core for all stations; **c** Shannon’s diversity  $H'(\log e)$  on core scale for all stations; **d** Simpson’s diversity  $1-\lambda$  on core scale for all stations; **e** rarefaction diversity  $ET(500)$  on core scale for all stations.  $ET(N)$  indicates an expected number of higher taxa for a given number of individuals

Interestingly, the innermost and outermost Larsen B stations ‘B West’ and ‘B South’ were similarly diverse for both indices.

Rarefaction values  $ET(500)$  on core scale corresponded with other diversity indices for stations ‘A South’ and ‘B Seep’. The  $ET(500)$  for ‘B West’, on the other hand, was much lower than for ‘B South’ (Fig. 4e). No diversity–depth gradient was visible for the deep-sea stations anymore. Instead, ‘A1000’ was very diverse, whereas the other three deep-sea stations exhibited similarly low diversity, comparable to  $ET(500)$  at ‘B West’.

Core-scale (median) and site-scale  $ET(500)$  values corresponded well with each other and with the median taxa numbers per core (Fig. 5). The high similarity of  $ET(500)$  values for ‘B East’ and ‘Elph’ was not surprising since only one core, or three cores, respectively, were available from these stations. Nevertheless, similarity also remained high for most other stations, even though sometimes up to 14 cores were available. Only the site scale  $ET(500)$  for ‘A South’, ‘B North’, and ‘A1000’ was slightly higher than the respective core scale  $ET(500)$  values. Hence, whether core scale or site scale was chosen did not matter much for our stations, which

**Fig. 5** Rarefaction diversity *ET*(500) on core scale (median) and site scale (single value) in comparison to the number of meiofaunal higher taxa per core (median); *vertical line* separates continental shelf stations from deep-sea stations



is sufficiently explained by the low taxonomic resolution of the available dataset.

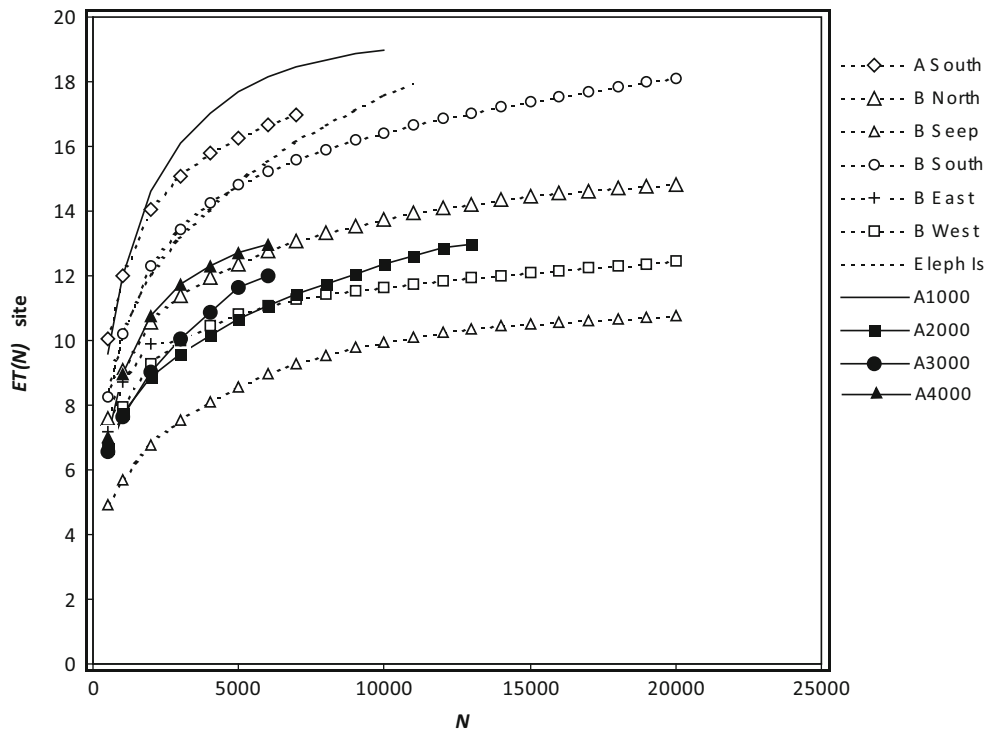
For comparisons of higher *ET*(500) values at site scale (cores pooled) rarefaction curves were plotted (Fig. 6). Station ‘A1000’ yielded the steepest curve on site scale, followed by ‘A South’. Asymptotic curves were not reached for stations with fewer cores (‘B East’, ‘Elph’, ‘A2000’, ‘A3000’), implying an undersampling issue with these stations.

Environmental factors

We investigated to what extent community patterns and parameters corresponded to a set of available environmental variables. On the level of single parameters (univariate), this

was done by regression analyses, whilst on community level (multivariate), canonical correspondence analyses (CCA) were performed. The whole set of environmental variables was not measured at all stations: comparable phytopigment data were available for station ‘Elph’ and the Larsen samples (Table S3; see also “Materials and Methods”). CPE concentrations in the upper 5 cm of sediment of the ANDEEP-2 stations (medians: ‘A1000’: 0.936 µg/g; ‘A2000’: 1.071 µg/g; ‘A3000’: 0.939 µg/g; ‘A4000’: 0.866 µg/g) were obtained by a different method and not considered for the environmental analyses in this section. Noteworthy, however, is that these values were comparably low, as is typical for the deep sea (e.g., Grant et al. 2002; 1–35 µg/g CPE for Arctic stations ranging 250 to 800 m water depth).

**Fig. 6** Site-scale rarefaction curves up to *ET*(20000) for all stations



Linear regressions of selected community parameters (number of observed taxa  $T$ , number of individuals  $N$ , Shannon's  $H'(\log e)$  richness index, Simpson's Evenness  $1/\lambda'$ , core-scale  $ET(500)$ ) on selected environmental factors (depth, volumetric mean of sediment grain size in the upper cm) yielded highly significant negative slopes (after correction for multiple tests) for depth versus  $N$ , and depth vs Shannon's and Simpson's diversity measures (Table S3). Highly significant positive regression slopes were found for volumetric mean versus all community measures except for  $N$ .

Ordination by CCA allowed a more detailed evaluation of data, by partly including phytopigments as a proxy for food supply and productivity.

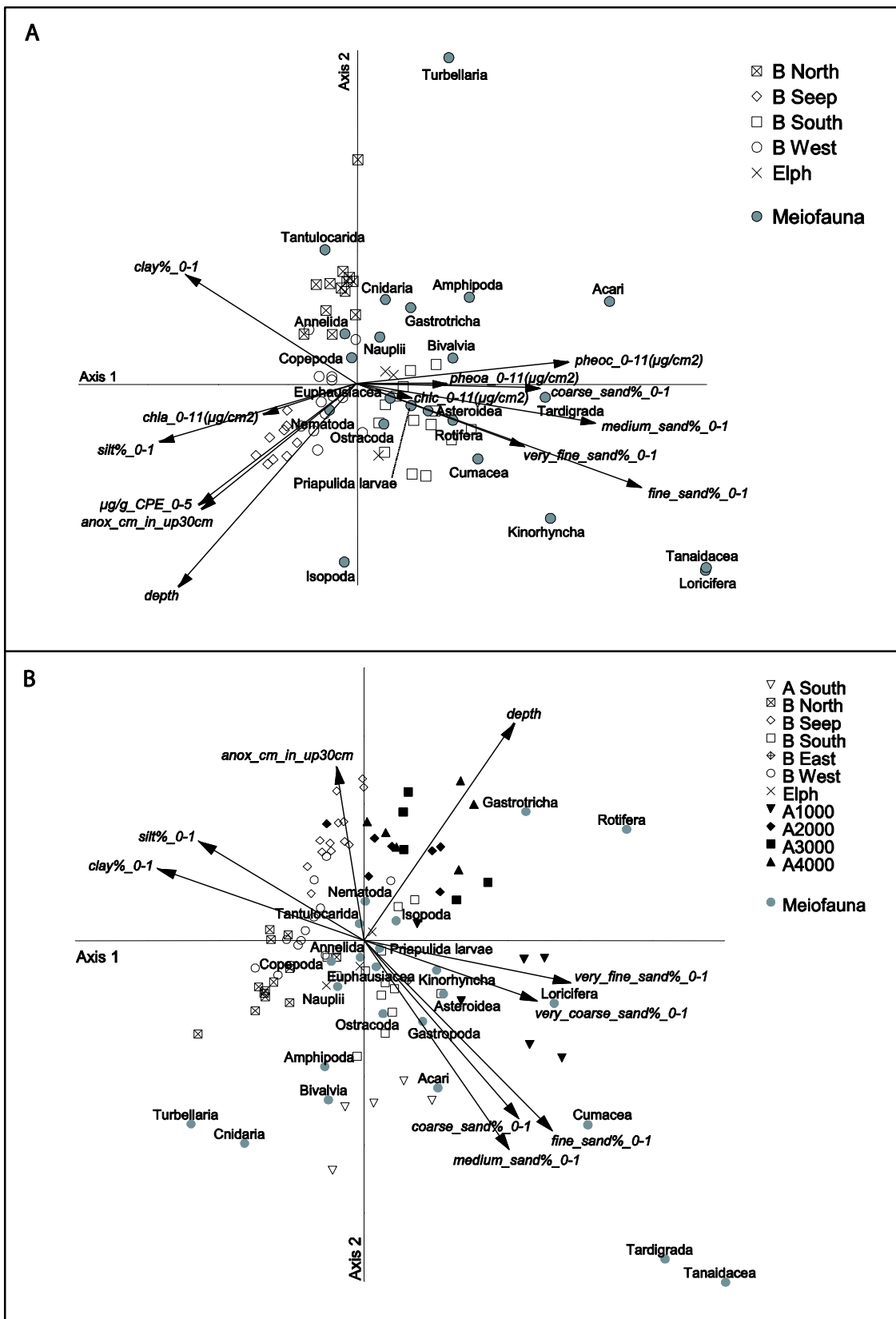
A first CCA was run on those stations where all 14 measured environmental variables were available ('B North', 'B Seep', 'B South', 'B West', 'Elph'). However, since no very coarse sand was found in the first cm of sediment at cores from these five stations, that variable was excluded from the analysis. The remaining 13 factors explained 53.1 % of the total inertia in the dataset (Table S4). The unexplained remainder of 46.9 % was due to unstudied/missing environmental factors, biotic factors, interactions, and noise in the dataset. A triplot visualized correlations between assemblage structures, stations, and environmental factors on the first two canonical axes (Fig. 7a). Different lengths of arrows indicate relative importance of a certain factor in explaining the total inertia in the dataset along the first two axes. Additional data for the third axis are given in Table S4. The first canonical axis explained 20.4 % of the total inertia, respectively 38.5 % of the explainable inertia (Table S4). The second axis showed only slightly less explanatory power (15.8 %, respectively 29.7%), whereas the third axis was less important (7.5 %, respectively 14.1 %). All other axes (not shown) accounted for 9.4 % of the total inertia, or 17.6 % of the explainable inertia, respectively. Factors strongly correlating with the first axis had greatest explanatory power for meiobenthic higher taxa distribution patterns, namely fine sand % and medium sand % in the upper cm of the sediment. The third-most important factor, depth, was the only one that showed strongest correlation with the second canonical axis, indicating that this variable explained a portion of inertia different from that explained by the other factors. Among phytopigments, the inventory of phaeophytin c in the upper 11 cm of sediment (strongly correlated with the first axis) explained most of the total variance. Factors mainly associated to the third axis were less important (Table S4). Site scores of stations aggregated very well in the triplot, but no clear separation between groups of stations was obtained (Fig. 7a). Nevertheless, since not only the community structure but also environmental factors were taken into account in the CCA triplot, a grouping of the selected stations was stronger than in the nMDS plot (Fig. 2), especially for 'B North' and 'B Seep' with their finer sediment structure.

A second CCA, excluding phytopigment variables not available for the deep-sea stations, was performed with all eleven stations (Fig. 7a, b). Only 33.4 % of the total inertia was explained by the environmental factors. The first canonical axis explained 12.4 % of the total, and 37.0 % of the explainable inertia (Table S4). The second axis explained slightly less inertia (10.4 %, respectively 31.2%), whereas the third axis was less important (4.6 %, respectively 13.8 %). All other axes accounted for 10.0 % of the total inertia (18.0 % of the explainable inertia). The explanatory power of the first three axes relative to the total explainable inertia was very similar to that of the first analysis; however, in relation to the overall inertia, explanatory powers of the axes were much lower when compared to the first CCA. In the second CCA, the proportion of fine sand in the upper sediment cm and depth were the factors that explained meiobenthic distribution patterns best. The vectors of both variables stood nearly orthogonally opposed, indicating that these factors complemented each other's explanatory power. In contrast to the first analysis, none of the variables showed highest correlation with the third axis. This was not surprising, since it was mainly the phytopigment variables not considered here that were predominately associated with the third axis of the first CCA.

Some meiofaunal higher taxa showed good correlations to certain environmental factors in both CCA analyses (only taxa with at least 50 individuals were considered here). Turbellaria were only recorded from the shelf stations (Table S1), likely explained by high destruction rates of their soft bodies when collecting from greater depths (Faubel and Noreña 2006). Many other groups also had lower densities at higher depths, moving the centroid of the CCA triplots into that direction. Only Rotifera showed an opposite trend. Habitats with higher average grain sizes (sandy habitats) were preferred by Kinorhyncha, Loricifera, Rotifera, Tanaidacea, and Tardigrada. Acari and Tardigrada showed higher abundances at stations with a high phaeophytin c inventory in the upper 1 cm of sediment. In summary, fine sand % and medium sand % in the upper cm of sediment, as well as depth, were the factors which best explained meiofaunal major taxa composition at the investigated shelf and deep-sea stations.

## Discussion

We proposed a set of hypotheses in order to test for a relative similarity of meiobenthic communities from Antarctic continental shelf stations differently influenced by former iceshelf coverage to stations from the Antarctic deep sea. It was suggested that, due to longer-term consequences of low productivity and food supply, meiobenthic communities of the innermost Larsen embayments should have a higher affinity to



**Fig. 7** Canonical correspondence analysis (CCA) triplots, showing inter-correlations between core-scale meiofaunal assemblage structures, site scores, and environmental factors for **a** five selected stations with 13

measured environmental variables, and **b** all eleven stations with nine selected environmental variables (see “Materials and Methods” for further details)

communities of the deep sea than do Larsen stations with intermediate distance to the former ice edge. Furthermore, we hypothesized that communities from the latter (intermediate) localities show a higher affinity to deep-sea communities than do those from the former shelf ice edge and the open shelf.

Regarding hypotheses *I* and *II*, similarity of meiofaunal communities from the sheltered innermost Larsen B embayment to the deep-sea was significantly higher than similarity of a former Larsen ice-edge station and an open shelf station near Elephant Island to the deep sea (Table 2), corroborating our assumptions regarding the differences in food supply between these stations. As for hypotheses *III–VI*, similarities of communities from the innermost Larsen B area to the deep-sea were still always significantly higher than similarities of most of the intermediate Larsen A and B stations to the deep-sea. However, station ‘B East’ was not significantly different from ‘B West’, probably owing to its position close to the former ice edge. In contrast to the nearby ice-edge station ‘B South’, communities at station ‘B East’ were likely cut off from nutrient-rich northerly currents of the Weddell Gyre by landmasses to the south. Regarding hypotheses *VII–XIV*, the similarity of the intermediate Larsen stations to the deep-sea was mostly significantly higher than similarities of the former Larsen ice-edge and open shelf communities to those of the deep-sea. Only two out of 32 tests were not significant, and both these tests included station ‘Elph’ from where only a few cores ( $n = 3$ ) were available leading to reduced testing power.

Meiobenthic communities of the Antarctic continental shelf stations could be ordered according to their resemblance with deep-sea stations: ‘B West’ > ‘B East’ > ‘B North’ > ‘A South’ > ‘B Seep’ > ‘Elph’ > ‘B South’, which is in accordance to our hypotheses. Surprisingly, the deepest Larsen station ‘B Seep’ (800 m) showed only intermediate resemblance to the deep-sea stations, presumably because it was close to a low-active cold seep (Domack et al. 2005b; Niemann et al. 2009). This special environment caused high mono-generic nematode densities that stand in stark contrast to the low nematode densities at the deep-sea stations and ‘B West’ (Hauquier et al. 2011). The position of ‘B Seep’ within a trough, which accumulates food deposition from surface waters, might have contributed to highest CPE concentrations of all the Larsen stations (Gutt et al. 2011; Hauquier et al. 2011; Sañe Schepísi et al. 2011), and hence added to the lower community resemblance with the nutrient-poor deep-sea stations.

Our test results indicate that a faunal gradient presents itself across the Larsen area, with meiobenthic higher taxa community composition close to the former iceshelf edge being much less similar to that of the deep sea than was the case for stations at intermediate parts of the former iceshelf and the innermost Larsen B embayment. Most striking was the high resemblance between communities of the innermost Larsen B area and those of the deep sea.

Antarctic continental shelf and deep-sea benthic communities

The environmental setting of Antarctic continental shelf and deep-sea communities is different from that of respective communities at lower latitudes. The Antarctic shelf is generally quite deep (Kaiser et al. 2011, 2013) and isostatically depressed down to 900 m depth in some places (Gage 2004), thus reaching bathyal depths. The possibility of faunal exchange between deeper and shallower zones is generally facilitated in Antarctic waters by coupling of the deep Antarctic continental shelf with submerging Antarctic bottom water and emerging circumpolar deep water, leading to ‘polar submergence’ of shelf fauna and ‘polar emergence’ of deep-sea fauna (Brandt 1992; Held 2000; Clarke 2003; Strugnell et al. 2011). This phenomenon and the presence of an extraordinarily rich macrobenthos on the Antarctic continental shelf has led to general hypotheses regarding significant exchange between the shelf and the deep sea on evolutionary time scales (e.g., Brandt 1992; Clarke 2003; Gage 2004). In this respect, Glover et al. (2008) found similarities of Antarctic continental shelf macrofaunal communities (polychaetes at family level) to those of the Atlantic and Pacific deep sea. Also, for the meiofauna evidence for such an exchange exists (e.g., Veit-Köhler 2004: copepods in the Weddell Sea; Gooday et al. 1996: foraminiferans of Explorers Cove), as eurybathic species may co-exist with species with limited depth distribution (e.g., Ingels et al. 2006: nematodes). Vanhove et al. (1997) reported a certain resemblance of meiobenthic shallow-water and deep-sea meiobenthic communities in Antarctic waters in terms of patchiness, standing stock, diversity, and their relation with the environment, even though density, total biomass, and number of meiofaunal higher taxa were still correlated with water depth. The results of our study are concordant with these findings, and we assume that polar emergence might have supported the establishment of deep-sea-like meiofaunal communities in the inner Larsen region during thousands of years with ice coverage.

On the other hand, a high proportion of isopod species was reported to be restricted to the Antarctic continental shelf (Brandt 1992). Also, Kaiser et al. (2011) found a distinct Antarctic slope fauna for certain marine groups, and as for cumaceans the species overlap between Antarctic shelf and deep sea was only 18 % (Mühlenhardt-Siegel 2011). Other studies suggest a high degree of eurybathic species, supporting the theory of an enhanced faunal connection in the Antarctic (e.g., Brey et al. 1996). In contrast, genetic studies revealed water depth as a strong barrier to gene flow in some lineages (e.g., Hunter and Halanych 2008). Though all this might hold true on species level, it is probably much less true on higher taxonomic levels and therefore not contradictory to our findings.

## Antarctic sub-iceshelf and deep-sea benthos

A considerable faunal resemblance of formerly iceshelf-covered Antarctic continental shelf communities to deep-sea communities has already been shown for macrobenthos of the Larsen B region on the species level (e.g., Gutt et al. 2011), as well as for nematodes of the same region on the genus level (Raes et al. 2010). Whether these observations hold true for meiobenthos in total on a higher taxa level has not yet been investigated, a gap which the present study fills.

In some areas of the deep Weddell Sea, relatively high meiofaunal densities were recorded compared to other deep-sea areas (Sebastian et al. 2007: explained by food supply). The same applies to shallow-water meiobenthos with high densities in the Antarctic compared to other oceans (Vanhove et al. 1997). Generally, meiofauna seems to be able to exploit the episodic food supply in Antarctic shallow and deep waters very efficiently (Vanhove et al. 1997). Food banks might integrate such episodic food supply on a temporal scale (Mincks et al. 2008), which helps to sustain an established meiofaunal community. In other regions of the world, differences between shallow-water and the deep-sea meiofauna can be more extreme. Harpacticoid copepod communities for example showed remarkably even distributions with extraordinarily high species numbers but low densities in the abyssal deep sea of the Angola Basin (Rose et al. 2005), whereas intertidal harpacticoid communities are sometimes strongly dominated by one or a few species with high densities (e.g., Rose and Seifried 2006), or may even be monospecific (George and Rose 2004). Highly different regimes of productivity, stability, and temperature are likely to explain these patterns. For the deep sea, Giere (2009) stated that the often extremely high local-scale diversity of deep-sea meiofauna may be caused by moderate fluctuations in oxygen regimes, small disturbance effects in a mosaic of variables, and narrow niches of the organisms, creating a factorial complex that maintains subtle ecological disequilibrium processes. This is surely valid on the species level, but probably much less so on higher taxa levels since we found relatively low numbers of meiofaunal higher taxa per core, high patchiness levels for certain taxa, and low *ET*(500) core-/site-scale rarefaction values at the deepest three deep-sea stations (Table S2).

## The role of environmental factors

We dealt with a mosaic of potentially influential environmental factors at the investigated stations. Three of these were of special interest for our study: food supply (A), sediment structure (B), and water depth (C). Each of these factor complexes was associated with a different orthogonal CCA axis (Table S4), indicating that they indeed reflected different ecological processes acting on Antarctic meiobenthos. The CCA provided an interesting mosaic piece to interpret

meiofauna distribution patterns, but the CCA unimodal taxon distribution model along environmental axes is likely more adequate for analyses on species level, since ecological preferences are most distinct on the level where niche separation occurs.

## *Food supply: meiofaunal densities and preferences after CCA*

Higher meiofaunal densities corresponded with better food conditions (Tables S2, S5). Food supply was reflected by CCA axis 3 (Table S5) which was correlated with most of the productivity variables. Food supply and densities were comparably low at the inner Larsen stations ‘B West’ (lowest food supply; Table S5), ‘B North’, ‘B East’, and ‘A South’, as well as at the four deep-sea stations (and at several other places of the Antarctic deep-sea: e.g., Gutzmann et al. 2004; Vanhove et al. 2004). In contrast, both densities and phytodetrital food supply were high at the ice-edge station ‘B South’ and the open shelf station ‘Elph’. The cold seep station ‘B Seep’ was somewhat exceptional in that it expressed low CPE concentrations, yet highest meiofaunal densities being dominated by nematodes. An explanation for this can be found in chemosynthetic productivity of the site which has only recently died down: most of the food supply here did not originate from algae (measured by CPE), but from bacterial metabolism.

Food supply and food quality in the deep sea is generally lower than in shallower waters, owing to the degradation processes organic matter undergoes during its descent to the sea floor. The poverty of food is often a limiting factor for benthic deep-sea communities globally. Food-restricted conditions influence the size structure of deep-sea communities (Thistle 2003), leading to greater relative numbers of meiofaunal organisms (Giere 2009). Gutt et al. (2011) proposed that the decomposition of organic matter during transit from open waters to areas beneath ice shelves is similar to that from the euphotic zone to the deep sea, leading to the assumption that life under ice shelves faces conditions akin to those in the deep sea, resulting in similar community characteristics. The food-poor conditions of iceshelf-covered habitats changed drastically after the iceshelf break-ups in the Larsen areas. Short but intense summer phytoplankton blooms suddenly resulted in strong episodic food supply, as reported for the Weddell Sea (Veit-Köhler et al. 2011) and the West Antarctic continental shelf (Smith et al. 2008: FOODBANCS project), and affected benthic community structure (e.g., Glover et al. 2008). However, the sediment ecosystem seems to integrate long-term variability in surface production processes over time scales of many months to years (Mincks et al. 2008), since food sources may be utilized as food banks by benthic organisms throughout the year (McClintic et al. 2008; Glover et al. 2008; Purinton et al. 2008). Food banks could have stabilized nutrient conditions

in the Larsen area, most probably near the former ice edge and in troughs, and this has likely led to higher meiofaunal densities at stations ‘B South’ and ‘B Seep’.

In addition, the high densities at ‘B South’ may have resulted from the very productive conditions characteristic for near-ice margins. Ice margins in the Arctic Ocean, for instance, produce large amounts of primary production that reach the deep sea (Fonseca and Soltwedel 2007; Hoste et al. 2007). Analogically, drifting icebergs are linked to local enrichment and higher carbon fluxes to the seafloor, implying substantial influence of ice margins on benthic ecosystems (Smith et al. 2011). Greater densities at Antarctic stations with higher food input were also recorded for nematodes of the deep Weddell Sea (Sebastian et al. 2007), and for meiobenthos in shallow waters of the Ross Sea (Fabiano and Danovaro 1999). Especially, nematodes seem to be very sensitive to changes in food availability, as shown for the Larsen area by Hauquier et al. (2011), and demonstrated here by the differences in nematode abundance dominating the results for the overall meiofauna. At the time of our study, a positive effect of increased food input on meiofaunal abundance was not yet observable for the innermost Larsen B embayment. Reason for this was that, even 5 years after iceshelf disintegration, phytopigment inventories and fluxes were still much lower at ‘B West’, compared to the ice-edge station ‘B South’ (Sañe Schepisi et al. 2011). However, in the long term, food supply is expected to increase considerably in the innermost parts of the formerly iceshelf-covered Larsen areas. Accordingly, an increase of meiofaunal densities will likely occur in the future, and this throughout the inner Larsen area and other Antarctic regions where iceshelf coverage is diminishing.

#### *Food supply: meiofaunal diversity*

According to the productivity–diversity hypothesis (Huston 1979, modified by Rosenzweig 1995), food conditions can modify meiofaunal diversity and composition. Although the modalities of productivity–diversity relationships are still being debated (Waide et al. 1999), a unimodal productivity–diversity curve seems prevalent (e.g., Huston and DeAngelis 1994; Rosenzweig and Abramsky 1993; Moens et al. 2013, for nematodes). However, evidence for a unimodal relation suffers from incomplete sampling across the full scale of productivity. Recently, Leduc et al. (2012) reported a unimodal productivity–diversity relationship for deep-sea nematodes in a study that included both ends of the productivity spectrum. It should be noted, however, that the peak or descending phase of a possible unimodal productivity–diversity relationship may not be exhibited for all taxa within the existing range of productivity in the deep sea (Rosenzweig 1995). According to these findings, we might have dealt with the ascending part of a unimodal productivity–diversity curve, at least for the inner Larsen area with its low to moderate food

supply. However, our study was based on a low number of higher taxa, and a positive food–diversity relationship was not clear (Table S2).

#### *Sediment structure: meiofaunal preferences after CCA*

Sediment structure correlated best to the first canonical axis of the CCA which explained most variation in the dataset (Table S4). It is well known from the literature that sediment structure influences meiofaunal distribution (e.g., Skowronski and De Corbisier 2002; Veit-Köhler et al. 2009; Coull 1985). Copepods, for instance, show a preference for coarser sediments, whereas finer sediments are preferred by nematodes (Giere 2009). Sandy habitats may contain up to 45 % pore volume (Giere 2009), which is more attractive for larger organisms (Williams 1972). In our study, CCA triplots indicated that Kinorhyncha, Loricifera, Rotifera, Tanaidacea, and Tardigrada preferred stations with higher average grain size (Fig. 7a, b), mostly in concordance with known preferences (e.g., Giere 2009). These taxa showed a more patchy distribution (Table S1: median-to-mean ratio), which might indicate a similarly patchy distribution of this sediment type in the area.

CCA axis 1 correlated best with very fine to medium sand in the upper cm of sediment which likely reflects the dominance of nematodes and their preference for finer sediment types. Slender burrowing organisms like nematodes are better suited to exploit the resources contained in the small interstitial spaces of the fine-particle sedimentary matrix which harbours a relatively larger amount of potential food-bearing surfaces compared to large-particle sediments. However, we found no special preferences of particular meiofauna taxa for fine, muddy sediments. Higher taxa which were present at muddy stations were mostly also prevalent at the more sandy stations, but not vice versa. Some higher taxa that occurred in sandy environments were absent in muddy environments, which could explain the higher taxon richness on core and site scale at the stations with coarser sediment structure.

#### *Sediment structure: meiofaunal diversity*

Sediment structure was also an important factor for meiobenthic higher taxa composition (Table S4). All diversity measures corresponded to the sedimentary factorial complex (Table S3). Diversity measures correlated very well with grain size within the first cm of sediment (Table S3), with higher diversity in coarser sediment (especially for ‘A1000’ and Larsen ‘A South’). However, Shannon’s and Simpson’s diversity measures did not differ much between the ecologically most distinct stations ‘B South’ (coarser sediment) and ‘B West’ (finer sediment), even though rarefaction values and numbers of higher taxa per core did.

### Water depth

Water depth was associated with the second canonical axis of the CCA (Table S4). Depth per se, or any unmeasured factor correlated with it, played an important role for shaping meiofaunal communities at the deepest stations. Lowest densities as well as lowest Shannon's and Simpson's diversity values were only measured at greatest depths ('A3000' and 'A4000', significant negative regression slopes of these parameters vs water depth, Table S3), whereas far more higher taxa were found at 'A1000' ( $T=19$ ) than at all other deep-sea stations ( $T=12$  or  $13$ , respectively.; Table S1). Since at the same time CPE concentrations and sediment structure did not differ much between the four deep-sea stations (Table S2; similar findings by Howe et al. 2004), depth remained as the only available factor to explain the density and diversity differences. This was also shown in the CCA triplot (Fig. 7b) where 'A1000' cores were separated from those of the deeper stations 'A2000' to 'A4000'. These two groups of deep-sea cores were, again, moderately separated from the Larsen and Elephant Island cores in the triplot.

Generally, meiofauna densities often decline with increasing water depth (Tietjen 1992), and our results confirmed such a relationship for the deep-sea stations. This pattern also holds true for many geographical regions (e.g., Pfannkuche and Thiel 1987: Svalbard shelf; Vincx et al. 1994: Northeast Atlantic; Herman and Dahms 1992; Vanhove et al. 1995: Eastern Weddell Sea; Baguley et al. 2006: Gulf of Mexico). Similarly, meiofauna diversity can also decrease with increasing water depth, leaving other ecological and evolutionary factors as possible drivers for observed diversity patterns (Danovaro et al. 2010). It is known that many biotic and abiotic factors correlate with water depth, so depth per se may not be the causative factor (Hoste et al. 2007). Food quantity and quality, and pressure, as well as temperature are among the more important variables concomitant with water depth. Based on the data used, no factor other than water depth was available to explain lowest densities at the deepest stations. Unmeasured food variables may have played an important role with, for instance, bacterial biomass potentially influencing meiobenthic communities, owing to preferential feeding strategies of certain taxa (Ingels et al. 2010). Furthermore, local chemical and biological enrichment associated with free-drifting icebergs could have increased downward export of food resources (Smith et al. 2007; Smith 2011) which, in turn, may have affected meiobenthic assemblages in the Larsen area on a local scale.

### Other factors

It is very likely that other abiotic (e.g., dissolved oxygen: Veit-Köhler et al. 2009) and biotic factors (e.g., mud concretions: Thistle and Eckman 1988; large motile epifauna: Thistle et al.

2008) were involved in structuring meiobenthic communities in the Larsen area. The amount of unexplained variation in the CCA analyses may be an indication for this (Table S4). Gutt et al. (2011), for instance, reported many deposit feeding holothurians (*Elpidia glacialis* THÉEL 1876) at station 'B Seep' which may exert grazing pressure on the meiofauna communities. One *Elpidia glacialis* specimen was found grazing in one of the MUC cores from that cold seep station. Interestingly, the number of nematodes and nauplii in exactly that core was reduced by a factor of 10 when compared to numbers in other cores from the same station, and the number of adult copepods, copepodites, and ostracods was reduced by factors of 2 to 3. This grazing impact on nematodes seems very plausible as the latter are ingested by holothurians with the sediment particles they reside in, and nematodes are not able to escape such 'predation'. Alternatively, bioturbatory disturbance or resource competition and resulting spatial segregation may be responsible (Ingels et al. 2014b).

### Taxonomic resolution and spatial scale

In the community nMDS plot (Fig. 2), the inner Larsen stations showed some overlap (Fig. 2). Hauquier et al. (2011) demonstrated that on the nematode genus level the separation of the same Larsen stations was more distinct (based on different MUC cores than our study). Since on smaller spatial scales a higher taxonomic resolution allowed us to distinguish between communities more efficiently, we think that the taxonomic resolution necessary to distinguish between communities is at least partly dependent on spatial scale (i.e., distance between stations). This is supported by data of Glover et al. (2008) who could distinguish polychaete communities of larger biogeographic regions even on family level. In their study biogeographic analysis of polychaete family-level composition from a range of globally distributed habitats indicated that, in general terms, geographic location was the most important factor in determining taxonomic composition. It has to be noted though that all taxonomic levels above species level are artificial concepts and any inference based on higher levels has to be treated with care.

### Outlook

The exposure of the Larsen A and B ecosystems to phytodetrital input implies the development of resident benthic communities influenced by colonization from adjacent areas. Re-establishment of certain macro- and megafaunal taxa and a strong decline of others may occur quite quickly (Hardy et al. 2011; Gutt et al. 2013). However, recolonization was shown to be slow for polar shallow-water meiofauna (Veit-Köhler et al. 2008), and food-driven and gradual for nematodes (Guilini et al. 2011; Raes et al. 2010; Boeckner et al. 2009), although selective settlement following



disturbance events may render colonization processes more efficient than originally anticipated (Lins et al. 2013). Generally, a complete re-establishment of open shelf benthic communities at previously iceshelf-covered areas was discussed to take hundreds to thousands of years (Post et al. 2007, 2011; Raes et al. 2010).

Concluding, 5 years after iceshelf disintegration the innermost embayments of the former Larsen iceshelf regions on the Antarctic continental shelf were inhabited by meiobenthic higher taxa communities that resembled Antarctic deep-sea communities. Food-poor conditions, typical for both habitats, coincided with low meiofaunal densities, and are likely responsible for the similarity in community characteristics. In contrast, meiofaunal diversity mainly coincided with grain size, a factor which is more related to hydrographic dynamics and currents than to former sub-iceshelf conditions. In order to evaluate the ongoing succession and patterns of recolonization, it would be of great scientific interest to track future community changes by continuing sampling effort in the Larsen A and B areas and other regions suffering iceshelf retreat and collapse caused by climate change. Although it might take centuries until meiofauna distributions reach new equilibria in the Larsen embayments, it is also possible that environmental conditions and meiobenthic community structures in the innermost parts of the formerly iceshelf-covered areas change much faster, as suggested by strong shifts in megabenthic communities between 2007 and 2011 in the Larsen area (Gutt et al. 2013).

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